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Mites (Acari) developing inside decomposing spruce needles: Biology and effect on decomposition rate

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Summary. Needles of spruce (*Picea abies*) were collected on snow, dried and placed on the forest floor in June. To be able to recollect the needles, they were fastened to strips of nylon mesh by putting each needle twice through the meshes. The strips were placed as naturally as possible in three different habitats: 1) Vegetation-free patches consisting of needle mats below trees, 2) Dense moss vegetation, and 3) Dense moss vegetation with bilberry (*Vaccinium myrtillus*). Needles were collected, dissected for mites, and weighed at eight samplings during a four year period. More than one third of the needles in each habitat became colonized by mites, probably by egg-laying in cracks produced by fungi. The juveniles excavated cavities inside the needles during their development. There were three species: *Steganacarus* cf. *striculus* (probably an undescribed species), *Rhysotritia ardua* and *Adoristes ovatus*. In the moss and moss/bilberry habitats, all species were present, but there was a strong dominance of *S.* cf. *striculus*. In the vegetation-free habitat, *R. ardua* was absent, and *S.* cf. *striculus* and *A. ovatus* were approximately equally abundant. Distribution of developmental instars showed that *A. ovatus* was the earliest colonisor, followed by *S.* cf. *striculus* and still later by *R. ardua*. Each species could have several (2–4) juveniles within the same needle, and some needles contained a mixed species composition. Up to three individuals of *S.* cf. *striculus* could develop successfully within one needle. At least *S.* cf. *striculus* and *A. ovatus* seemed to need 2 years to complete their development. In the moss and moss/bilberry habitats, needles containing juvenile mites showed a significantly slower dry weight loss compared to mite-free needles. It is suggested that the excrements of the juveniles, filling up parts of their cavity, may be subject to very slow decomposition. These excrements may be important in humus formation.

Key words: Decomposition rate, spruce needles, Acari, colonisation, excavation, excrements

Introduction

Most forests in Norway are coniferous forests, with spruce (*Picea abies* (L.) Karst.) as the dominant tree species. Because the major part of the litter fall from spruce trees consists of needles (Mork 1942, Bonnevie-Svendsen & Gjems 1957), the decomposition of spruce needles is a key process in the nutrient cycling in these forests. Spruce needles decompose, however, very slowly (e.g. Hågvar 1991, Johansson 1994), and a considerable raw humus layer may build up in the forest floor. Little is known about the contribution of soil animals in the decomposition of spruce needles. The most common spruce forest type with bilberry (*Vacci-*

nium myrtillus L.) vegetation, which is the focus in the present study, is almost without earthworms (Abrahamsen 1972 a), but has high densities of Enchytraeidae (Abrahamsen 1972 b), Collembola (Hågvar 1982) and Acari (Hågvar & Amundsen 1981). A ten year litter bag study on the succession of microarthropods among decomposing spruce needles (Hågvar 1991), and further dissections of needles, revealed that juveniles of certain oribatid mites (*Steganacarus* sp.) develop inside seemingly intact needles by excavating them. This motivated a closer, long term study on the role of needle-excavating mites on the decomposition of spruce needles.

Several oribatid mites have been shown to develop by excavating cavities within decomposing woody material (twigs, bark fragments, cone scales, etc.), or inside coniferous needles. Species in the genera *Steganacarus, Phthiracarus* and *Rhysotritia* among the "box mites" (Euptyctima) are often found to have such a cryptic juvenile life (e.g. Jacot 1939; Hartenstein 1962; Wallwork 1967; Pande & Berthet 1973; Webb 1977; Harding & Easton 1984; Ponge 1988; Berg 1989,1991; Fukuyama & Ito 1992). A non-box mite, *Adoristes ovatus* (C. L. Koch), is known to develop within coniferous needles (e. g. Jacot 1939; Gourbière et al. 1985; Lions & Gourbière 1988).

The quantitative role of juvenile mites excavating needles seems to be unknown. In the present study, their role was quantified by following decomposing spruce needles during four years, and insight was gained into the biology of three species in the genera *Steganacarus, Rhysotritia* and *Adoristes.*

Materials and Methods

Study site and habitats

The study site, situated on a flat plain of glacifluvial sandy deposits about 40 km N of Oslo, had an *Eu-Piceetum Myrtilletosum* vegetation type and a podzol soil (Typic Udipsamment, USDA classification). The pH of the raw humus was approximately 3.9. Spruce was the only tree species and had a height of 10–20 m. Three different ground habitats were chosen:

1. *"Moss vegetation"*: The ground had a dense moss cover, dominated by *Pleurozium schreberi* (Brid. Mitt.). There were two experimental sites, named Moss I and II (each approximately 50 m^2).
2. *"Bilberry vegetation"*: There was also a dense moss vegetation here, partly *Pleurozium schreberi*, and partly *Hylocomium splendens* (Hedw.) Schimp. In addition, there was a field layer of bilberry. There were two experimental sites, named Bilberry I and II (each approximately 50 m^2).
3. *"No vegetation"*: Below certain large spruces, there existed a vegetation-free "needle mat" of 1–2 m^2. Within an area of approximately 100 m^2, 8 vegetation-free patches were chosen for experiments.

All experimental sites were fenced to protect the ground from trampling by humans and animals.

Experimental design

Newly shed spruce needles were collected on snow during late winter, and dried at room temperature. In order to be able to recollect the needles after placing them on the ground, the needles were fixed to 80 cm long and 4 cm broad strips of nylon mesh. The needles were fastened by putting them twice through the meshes (Fig. 1). In each of the five experimental sites, 40 strips were placed in parallel rows 20 cm apart. In the vegetated plots, the strips were laid down in furrows gently made in the moss cover. The needles were placed horizontally, and both sides of the strip were bent upwards. In this position, the needles were „hanging" in the nylon strip, and had at the same time contact with the underlying substrate. The moss rapidly grew over the split in the vegetation. Later controls revealed that newly shed needles hang for several months in the green moss, and that the starting point of the needles in the strips was a little too deep. However, after one year, the vertical position was comparable to that of naturally shed needles. In the vegetation-free patches, the strips were laid flat on the top of the needle mat and fixed by small sticks. Here, the strips were gradually covered by new litter.

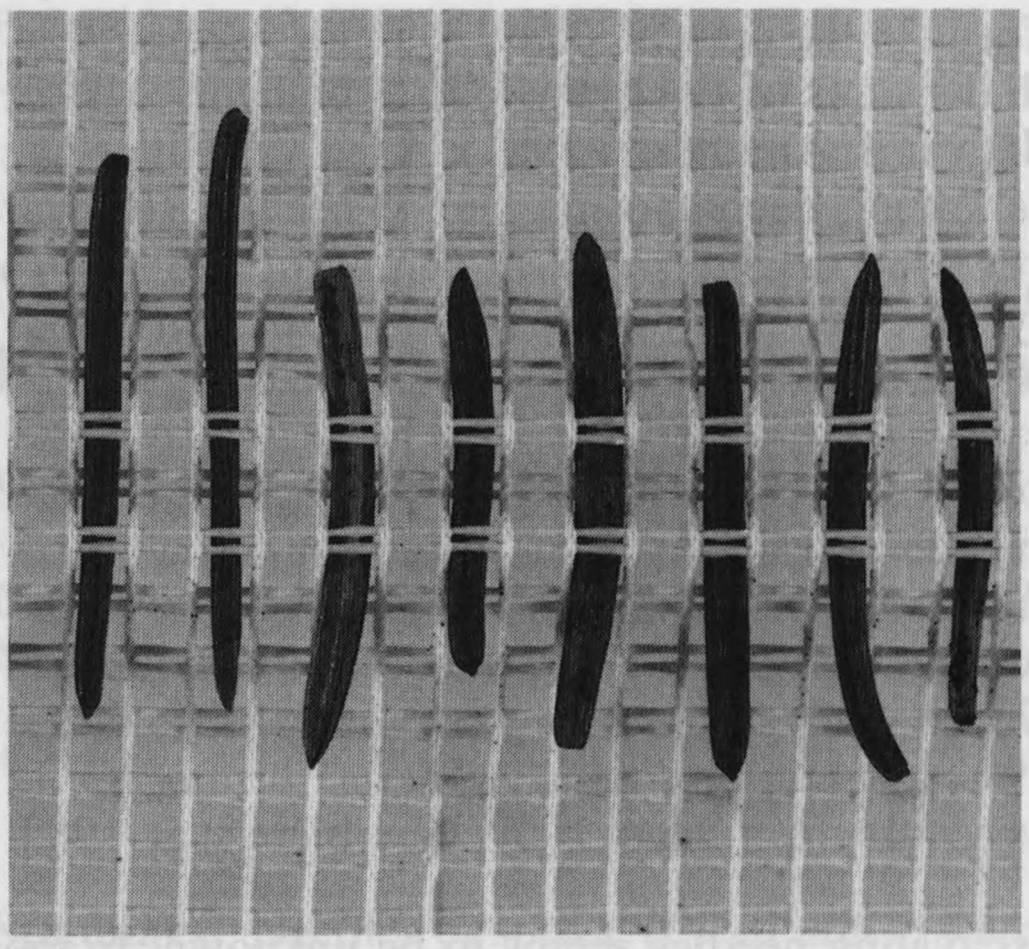

Fig. 1. To be able to record the needles, they were fastened to strips of nylon mesh before being placed in the field

Sampling procedure and study of mites in needles

The needles were placed in the field around 20 June 1986. Samplings were made on the following dates: I: 17 Oct. 1986, II: 30 June 1987, III: 2 Nov. 1987, IV: 17 June 1988, V: 18 May 1989, VI: 28 Aug. 1989, VII: 19 Oct. 1989, VIII: 8 Oct. 1990. The frequent sampling in 1989 was made to clarify the emergence time of the first adult mites.

At each sampling, four random strips were taken from each of the five sites. To ensure that mites within needles remained in their position until they could be studied, the strips were frozen in the field by solid CO_2 and brought to a freezer for storing. From each of the four first samplings, 100 needles from each strip were dissected for mites, which makes 400 needles per study site. The rest of the needles were used for other purposes (microbiology and chemistry). At later samplings, a lower number of needles was opened (Table 1). However, because a high percentage of the needles con-

Table 1. Percentage of spruce needles containing mites. Values in brackets are minimum values. n = number of needles investigated. The needles were laid out 20 June 1986

Sampling no.		I	II	III	IV	V	VI	VII	VIII
Months since start		4	12	16	24	35	38	40	52
Moss I		*0.8*	*2.8*	*14.0*	*21.3*	*41.5*	*53.5*	*42.6*	*(42.6)*
	n	400	400	400	400	200	200	195	190
Moss II		*0.5*	*1.3*	*11.8*	*17.5*	*45.0*	*29.0*	*35.5*	
	n	400	400	400	400	200	200	200	
Moss, mean values		0.7	2.1	12.9	19.4	43.3	41.3	39.1	(42.6)
Bilberry I		*1.5*	*1.0*	*11.5*	*19.8*	*32.0*	*32.0*	*39.0*	*(22.7)*
	n	400	400	400	400	200	200	200	128
Bilberry II		*2.0*	*4.5*	*20.3*	*23.3*	*39.5*	*41.0*	*39.0*	
	n	400	400	400	400	200	200	200	
Bilberry, mean values		1.8	2.8	15.9	21.6	35.8	36.5	39.0	(22.7)
No vegetation		*0.5*	*0.5*	*8.8*	*7.3*	*27.5*	*27.0*	*33.0*	*36.0*
	n	400	400	400	400	200	200	200	200

tained mites in this phase (Table 1), the number was considered sufficient. Dissection of needles was performed under a stereomicroscope, using two very pointed forceps. Slides of mites were made immediately.

Only unfragmented needles were dissected. There were two reasons for this. Firstly, to be sure that the juvenile mites found inside needles were really developing there and were not casual visitors from outside. Secondly, to be able to compare the dry weight of needles with and without mites. The dry weight of needles with mites included the excrements, but not the mites. There was no significant difference in length or width of needles with or without mites.

During 1989, adults of three oribatid mite species were found within needles. As these needles had no holes in the cuticula, the animals must have developed inside them. Most specimens were light in colour, indicating recent moulting. The same three species emerged from needles which were taken from strips and brought into the laboratory in late 1989 for hatching. The species were:

1. *Steganacarus* cf. *striculus* (C. L. Koch). According to Peter Gjelstrup (pers. comm.), it is a new species which will be described by him.
2. *Rhysotritia ardua.*
3. *Adoristes ovatus.*

The two first species belong to the so-called "box mites" (Euptyctima), the first to Phthiracaroidea and the second to Euphthiracaroidea. The third belongs to Liacaridae.

Juveniles of *S.* cf. *striculus* were identified from cultures. Adults were kept for egg-laying together with needles (which had been collected on snow and stored dry) on moist plaster of Paris, and slides were made from juveniles which developed inside the needles. The identification was confirmed by a slide from field material, where a tritonymph in ecdysis also showed the adult cuticula. According to Berg (1989), juveniles of Phthiracaroidea and Euphthiracaroidea are very similar. However, one difference is a pointed abdomen end in Phthiracaroidea, while the juveniles of Euphthiracaroidea have a rounded abdomen end. The pointed abdomen was confirmed in juveniles from cultures of *S.* cf. *striculus.* Corresponding cultures of *R. ardua* were not successful, but juveniles with a rounded abdomen (and longer hairs) were considered to belong to this species. The non-boxmite juveniles found in the needles were considered to belong to *A. ovatus*, the only non-box mite which hatched from needles. While the box mite juveniles are white, the *Adoristes* juveniles are more brownish and can easily be recognized even macroscopically.

Figs. 2–3 illustrate various developmental stages of *A. ovatus* and *S.* cf. *striculus,* partly in the needle and partly as slides. All juveniles were identified to developmental stages. While larvae were identified by having only three pairs of legs, protonymphs, deuteronymphs and tritonymphs were identified by having one, two or three pairs of genital suckers.

Laboratory cultures

Two cultures of S. cf. *striculus* were established on moistened plaster of Paris to more closely study the developmental rate. The first culture was kept at 15 °C, the other at temperatures which corresponded to mean monthly field temperatures in the raw humus. In both cases, the cultures started by allowing a number of newly extracted adults to lay eggs in needles during a three week period at room temperature. The culture at 15 °C started in September 1988 with 102 adult mites. After the removal of the mites, four samplings were made of juveniles inside needles: after three, five, seven and nine months.

The culture at natural temperatures started in June 1989 and was run for nearly two years. Mean monthly temperatures in raw humus at 2 cm depth were determined during the preceeding year: November-May: 0–2 °C (1 °C was used), June 12 °C, July 15 °C, August 11 °C, September 8 °C, and October 7 °C. During the culture's second winter, 4 °C was used instead of 1 °C for practical reasons.

Statistical tests

The distribution of mites in different parts of the needle (mid part or end parts) was investigated by chi-square test. Whether two species occurred in the same needle more often or more rarely than on a random base, was tested by Binomdist function in EXCEL 4.0, cumulative variant. Differences in the dry weight of needles with or without mites was tested by a paired t-test with four pairs, referring to four strips.

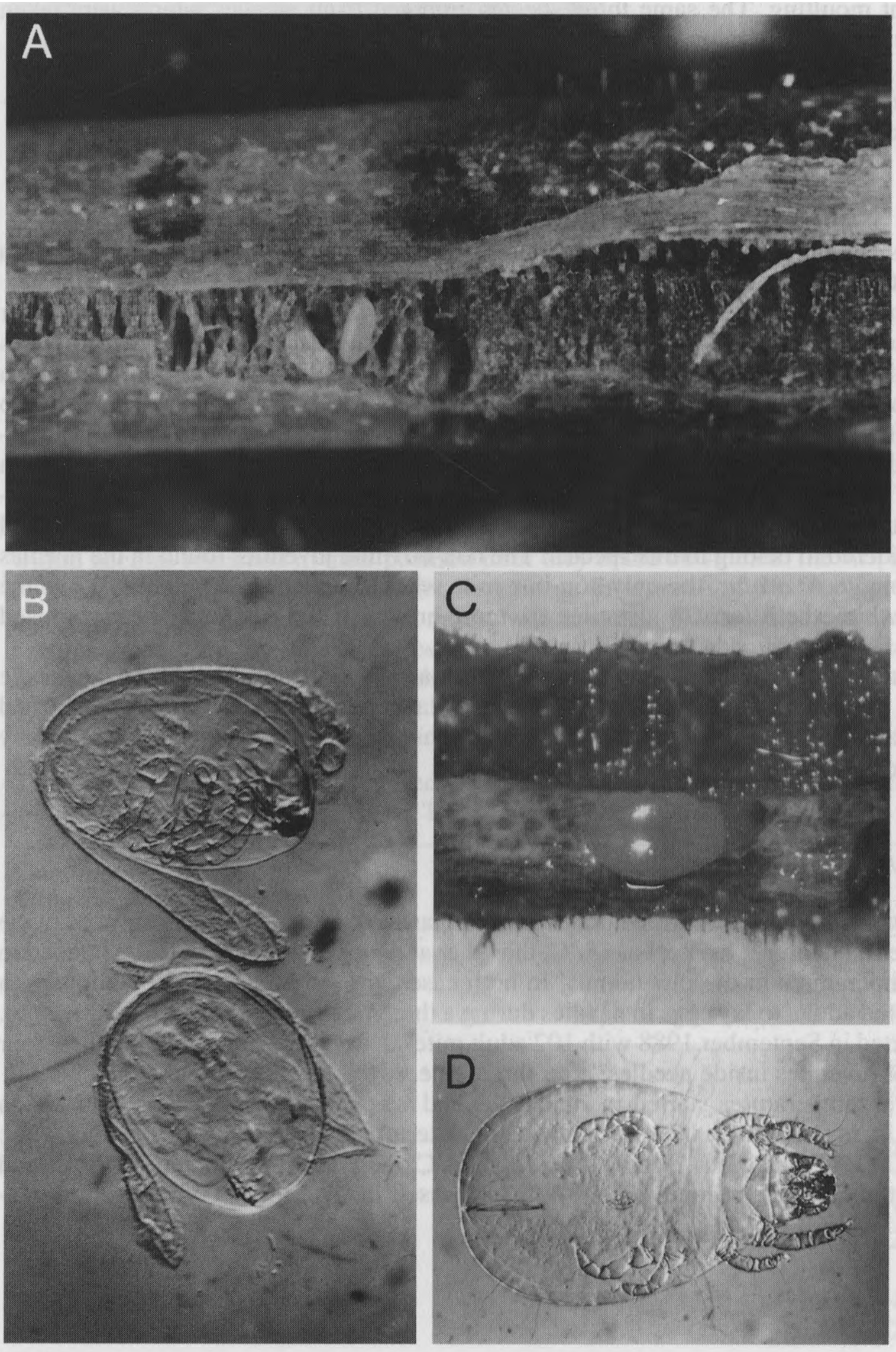

Fig. 2. Developmental stages of *Adoristes ovatus*. A: two newly laid eggs in a partly opened needle. B: eggs under hatching. C: deuteronymph within its cavity in an opened needle. D: slide of tritonymph

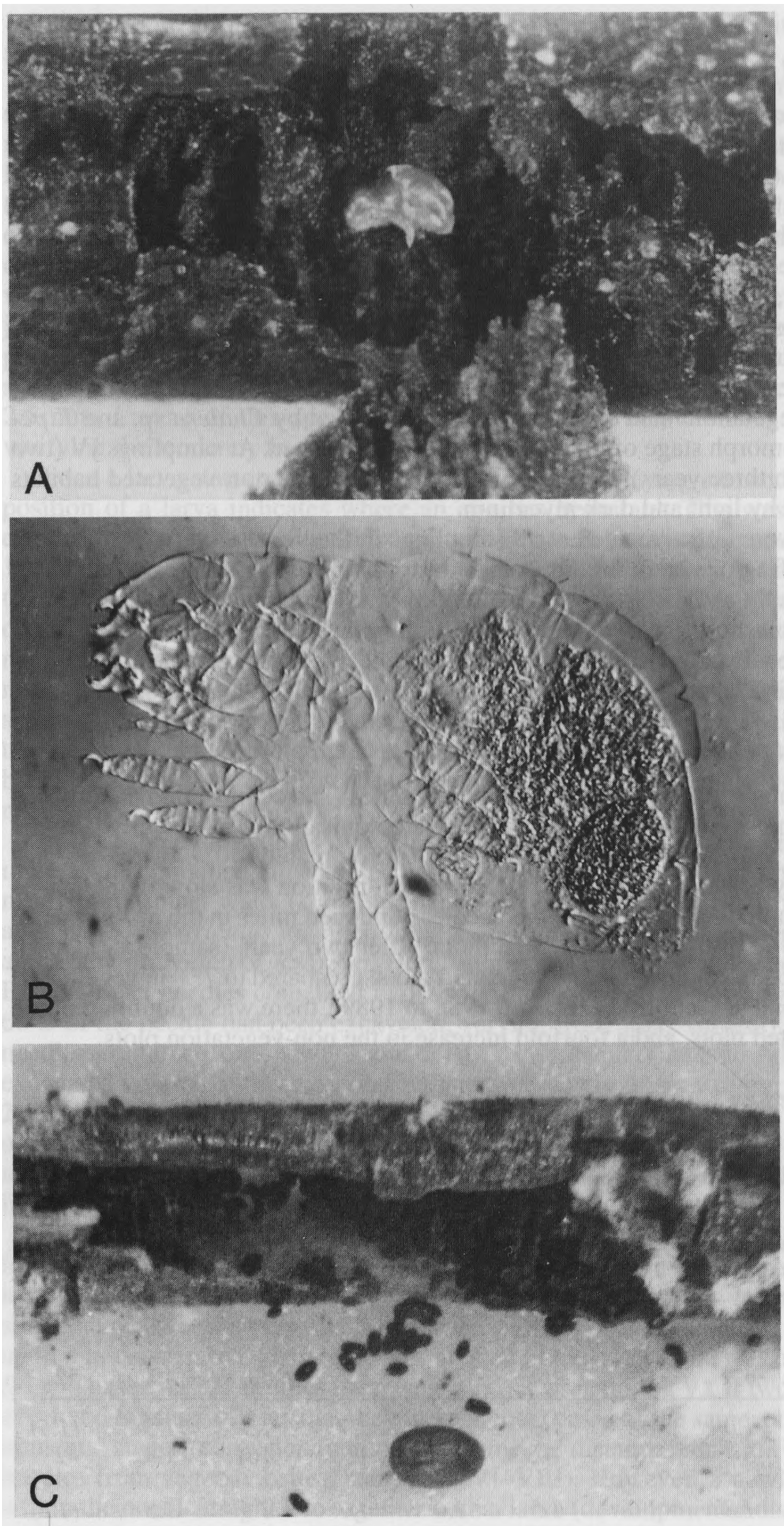

Fig. 3. Developmental stages of *Steganacarus* cf. *striculus.* A: larva in opened needle. B: slide of deuteronymph. C: a fully developed adult together with excrements, picked out from its cavity

Results

Fungal colonisation and fragmentation of the needles

Needles collected on snow were often already attacked by *Lophodermium piceae* (Fuckel) Höhnel, visible by the anamorph leptostoma stage and black lines. Some needles also contained *Tiarosporella parca* (Berk. and Br.) Whitney, Reid and Pirozynski, which was visible as small, round, black spots with pyknidia. Both these species are endophytic and colonize green needles. After four months on the ground (sampling I), the large, black teliomorph stage of *L. piceae* was visible on needles situated in vegetated habitats, but was still mainly in the imperfect stage in the drier, vegetation-free sites. At this time, several needles in the vegetated habitats were more or less covered by "brushes" from *Chalera* sp. and *Thysanophora penicillioides* (Roum.) Kendrick, while the epiphytic species *Rhizosphaera kalkhoffii* Bub. was observed on some needles in vegetation-free patches. After one year on the ground (sampling II), the needles in "no vegetation" had also been visibly colonized by *Chalera* sp. and *T. penicillioides*, and the teliomorph stage of *L. piceae* was fully developed. At samplings IV (two years) and VI (more than three years), needles in both vegetated and non-vegetated habitats were also partly covered by light and dark mycelium.

While most needles were unfragmented at all samplings in the vegetation-free site, about half of the needles were fragmented in the vegetated sites in samplings V–VII, and a majority at sampling VIII. Especially at the last sampling, the selection of non-fragmented needles represents a considerable bias in the vegetated sites. Assuming that needles with cavities fragment easier than other needles, the percentage of colonized needles may have been considerably underestimated (as indicated in Table 1 and Fig. 10).

Colonisation pattern and percentage of needles colonised

Table 1 shows the percentage of needles which contained mites. The colonisation pattern was very similar in the four moss and bilberry sites, while the colonisation was slower where the vegetation was lacking. However, in all habitat types, approximately 40 % of the needles were finally colonised by oribatid mites. In all sites, the colonisation was slow in the beginning. After one year (sample II), 1.0–4.5 % of the needles contained mites in the moss and bilberry plots, but only 0.5 % in the vegetation-free plots. After two years (sample IV), about 20 % of the needles had been colonised in the vegetated plots, compared to 7 % in vegetation-free plots. From the second to the third year (from 1988 to 1989), there was a doubling of the percentage in the vegetated plots, and a fourfold increase in the non-vegetation plots.

The content of single needles

The mean number of mites per needle containing mites is given in Table 2. Very often, two juveniles were found in the same needle, and the mean number per needle stabilised at about

Table 2. Mean number of mites per needle containing mites, at different samplings. Values in brackets are minimum values. n=number of needles with mites. The needles were laid out 20 June 1986.

Sampling no.		I	II	III	IV	V	VI	VII	VIII
Months since start		4	12	16	24	35	38	40	52
Moss		*1.0*	*1.8*	*1.6*	*1.4*	*1.7*	*1.5*	*1.5*	*(1.5)*
	n	5	16	103	155	173	161	136	42
Bilberry		*1.8*	*1.0*	*1.5*	*1.6*	*1.7*	*1.6*	*1.5*	*(1.3)*
	n	14	22	127	167	137	136	83	21
No vegetation		*1.0*	*1.0*	*1.7*	*1.3*	*1.6*	*1.4*	*1.7*	*1.6*
	n	1	2	35	29	55	54	62	59

1.5 in all three habitats. Sometimes, 3 or 4 juveniles occurred within one needle, with a maximum of 6.

Eggs were occasionally observed, and their exact position in the needle was noted during the two first samplings. The eggs had a characteristic cross-striated surface, and in two cases they were in the hatching phase, so that the larva of *A. ovatus* could be recognized (Fig. 2B). In 25 of 30 needles with eggs, the eggs were found inside longitudinal cracks formed by the teliomorph stage (black spots) of the fungus *Lophodermium piceae*. In the remaining 5 cases, eggs were placed in various natural cracks in the needle surface. This indicates that the mites do not make holes for egg-laying themselves, and it is not possible to predict from the outside whether a needle contains eggs or juveniles. As long as the needle does not fragment, the juveniles can develop within the needle rather safe from predators, as the needle wall is very persistent. Sometimes, two or three eggs were recorded side by side. In one case, as much as six larvae of *A. ovatus* were found within one needle, under natural cracks over a distance of 2.5 mm. Larvae of this species were also observed below cracks created by the fungus, verifying the tendency to deposit eggs in such cracks.

Since a larva starts excavating its cavity at the egg-laying site and is rather sedentary, the position of a larva indicates where an egg has been laid. This was used to study whether eggs were laid in the medium third part of the needle, or near the ends of the needle. Among 188 larvae of *S.* cf. *striculus,* there was no statistical difference in their distribution between three equal parts of the needle (mid part and end parts). This means that egg-laying had occurred randomly along the needle. However, egg-laying of *A. ovatus* tended to occur more near the ends than near the middle of the needle. Based on 45 larvae, the middle part of the needle had significantly fewer mites than one end of the needle ($P < 0.02$) and close to significance compared to the other end of the needle ($P < 0.07$). There was no attempt made to distinguish between the inner and outer end part in these studies, but according to Gourbiere et al. (1985), *A. ovatus* tends to place the egg at the petiole, i.e. the inner end of the *Picea* needle.

At least three individuals of *S.* cf. *striculus* can develop within a needle. One needle with intact walls contained three adults, and about 3/4 of the volume had been excavated. Another needle with intact walls (showing that no mites had entered from outside) contained three adults of *S.* cf. *striculus* together with two juvenile mites: a protonymph of the same species and a deuteronymph of *R. ardua*. Here, approximately 2/3 of the needle had been excavated. Eleven intact needles contained two newly developed adult *S.* cf. *striculus* each. A mean of 60 % of the needle had been excavated, varying from approximately 30 to 75 %. Fifty intact needles contained one newly developed *S.* cf. *striculus* and no other mites. The average excavated volume of these needles was approximately 40 %, varying between approximately 20 and 100 %. Newly developed adults of *S.* cf. *striculus* evidently stay for a while in the needle before they leave it, since many adults were recorded within intact needles. The reason is probably that they need time to harden their exoskeleton, as many of these adults had a light colour.

Figs. 4–7 illustrate how the content of single needles may vary, both concerning number of individuals, distribution of developmental stages, and the occurrence of two or three species together. For this purpose, data from moss and moss/bilberry vegetation have been fused, since the picture was very similar in these sites. In needles where *S.* cf. *striculus* was alone, up to 4 mites occurred per needle, but in 60 % of the cases there was only one mite per needle (Fig. 4, based on 227 needles from vegetated sites, sampling V). If two individuals of this species lived together in a needle, they were in most cases of the same, or of neighbouring developmental stages (corresponding to developmental distance 0 or 1 in Fig. 5, data based on 118 needles from vegetated sites, samplings VI–VIII). However, a newly developed adult, still within the needle, might live together with a larva (developmental distance 4 in Fig. 5). In 45 needles which all contained a newly developed adult of *S.* cf. *striculus* and at least one other mite, the accompaning mites were mainly tritonymphs of the same species, but all the other developmental stages could be found. Even various developmental stages of the two other species were recorded (Fig. 6, based on samplings VI–VIII, vegetated sites).

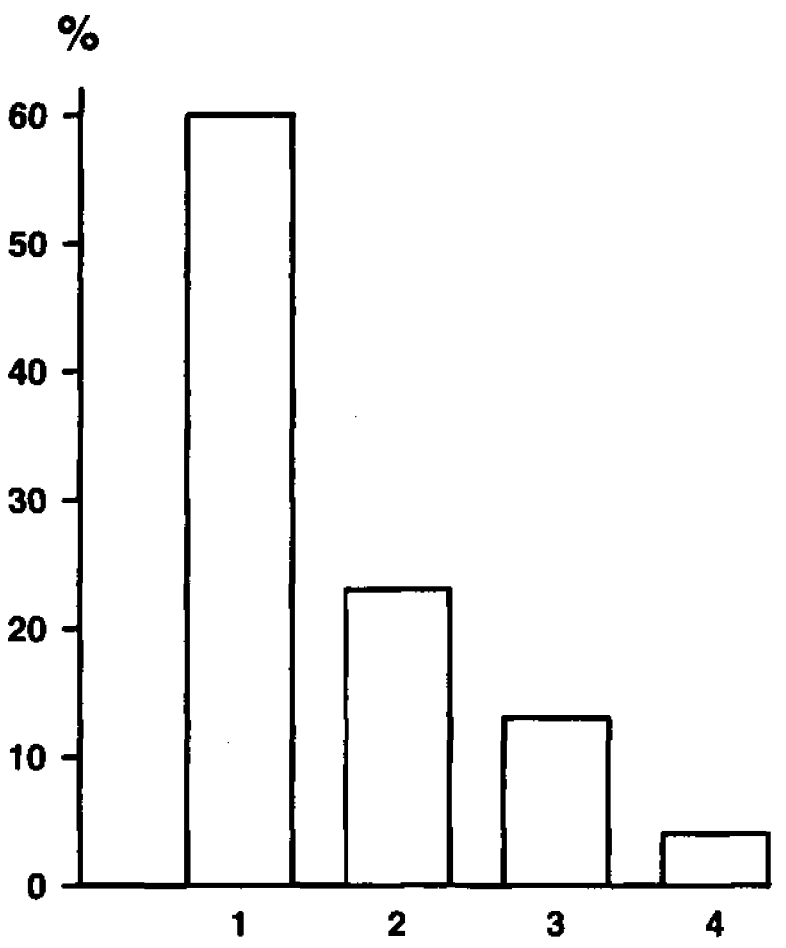

Fig. 4. In needles where *Steganacarus* cf. *striculus* was the only species, there were up to four mites per needle, but most often only one

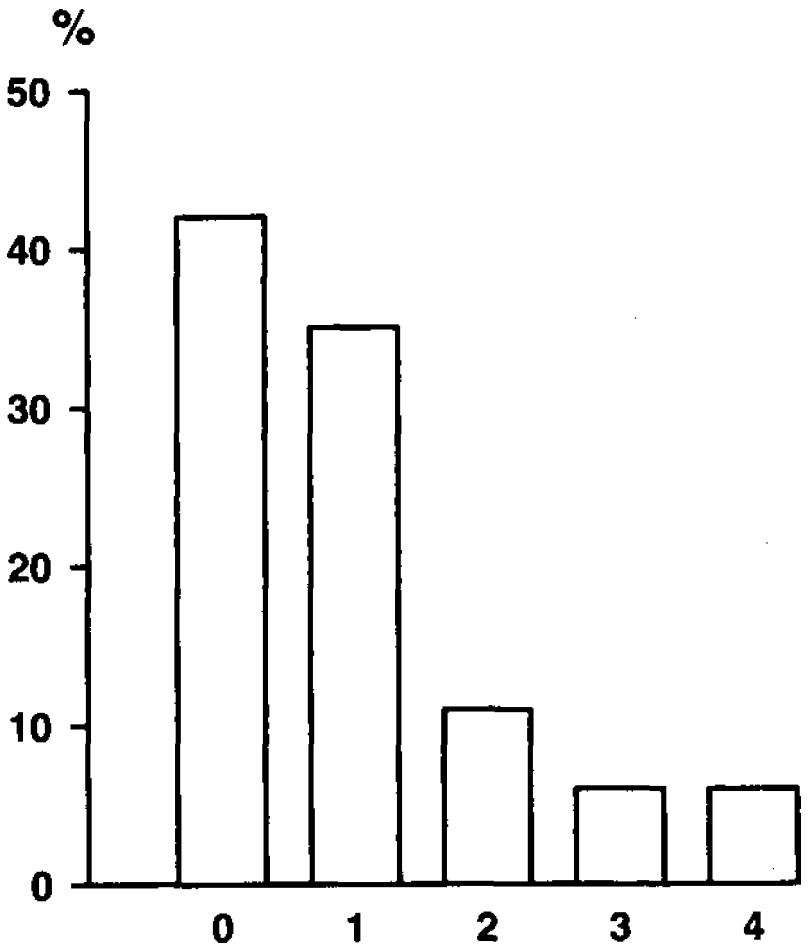

Fig. 5. In needles where two individuals of *Steganacarus* cf. *striculus* lived together, these individuals were most often in the same, or neighbouring developmental stage, corresponding to developmental distance zero or one

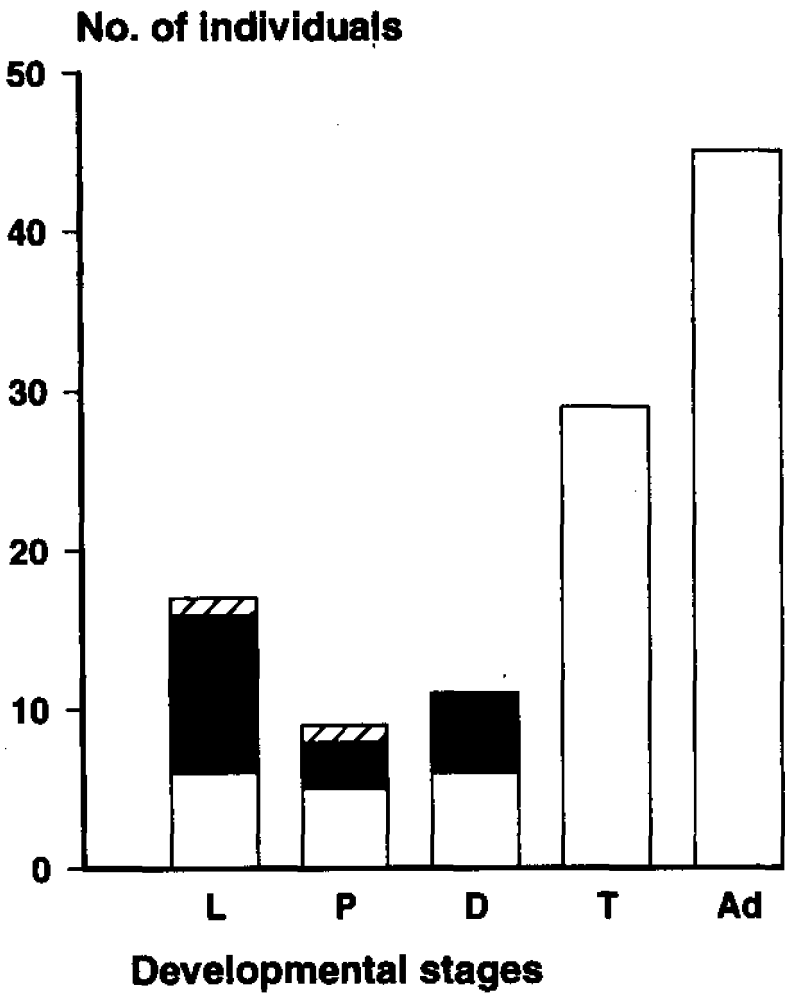

Fig. 6. In needles containing a newly developed adult of *Steganacarus* cf. *striculus,* and at least one other mite, the concurrent individuals were mainly tritonymphs (T) of the same species. However, larvae (L), protonymphs (P), or deuteronymphs (D) of various species might be present. White columns = *Steganacarus* cf. *striculus,* black columns = *Rhysotritia ardua,* hatched columns = *Adoristes ovatus*

Sometimes, two or three species occurred in the same needle. Data from moss and bilberry sites at sampling V showed that the most usual combination was one individual of the most common species *S.* cf. *striculus,* together with either one individual of *A. ovatus* or one individual of *R. ardua* (Fig. 7). Of 38 needles with mixed species composition, these two combinations made up 20 needles. Fourteen different combinations of species and individual numbers were found, with up to five mites per needle. Only in one needle did all three species occur together (Fig. 7).

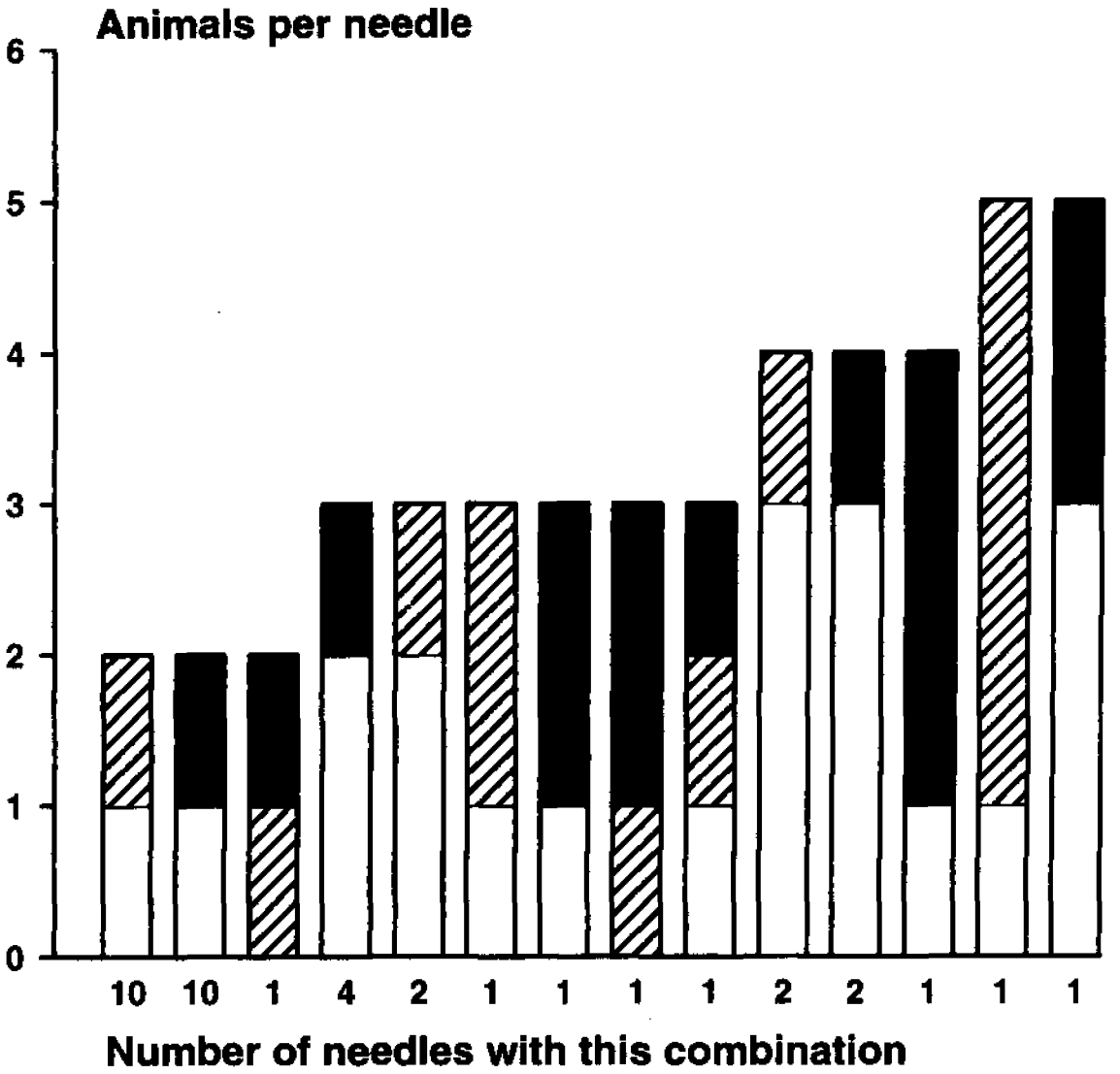

Fig. 7. Needles with more than one species contained up to five individuals. Fourteen different combinations were found. The most frequent combinations were one individual of *Steganacarus* cf. *striculus* (white columns) together with either one individual of *Rhysotritia ardua* (black columns) or *Adoristes ovatus* (hatched columns)

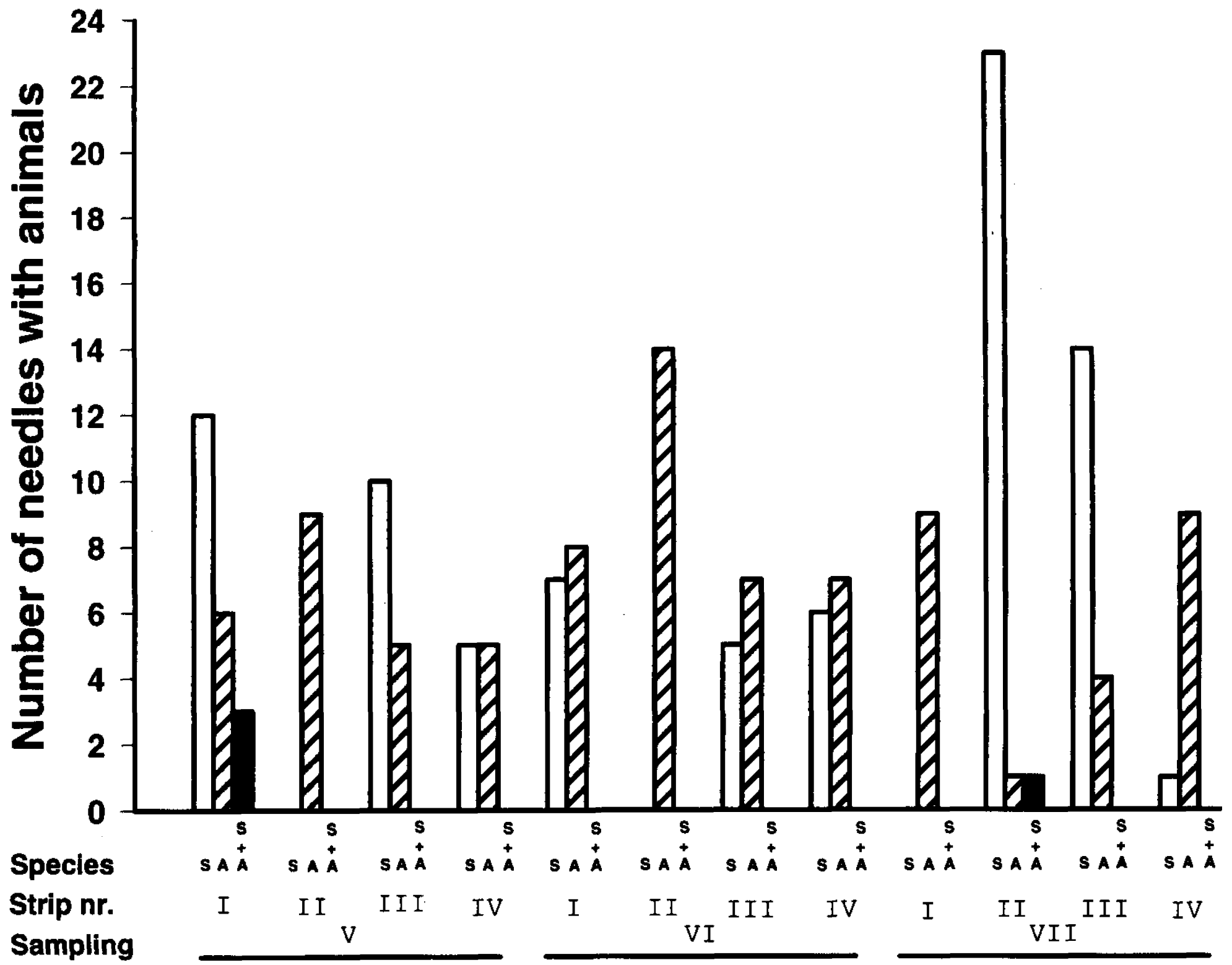

Fig. 8. In the vegetation-free plots, very few needles contained both *Steganacarus* cf. *striculus* (S) and *Adoristes ovatus* (A), see black columns. Several of the strips harvested during samplings V, VI and VII were dominated either by *S.* cf. *striculus* (white columns) or A. ovatus (hatched columns)

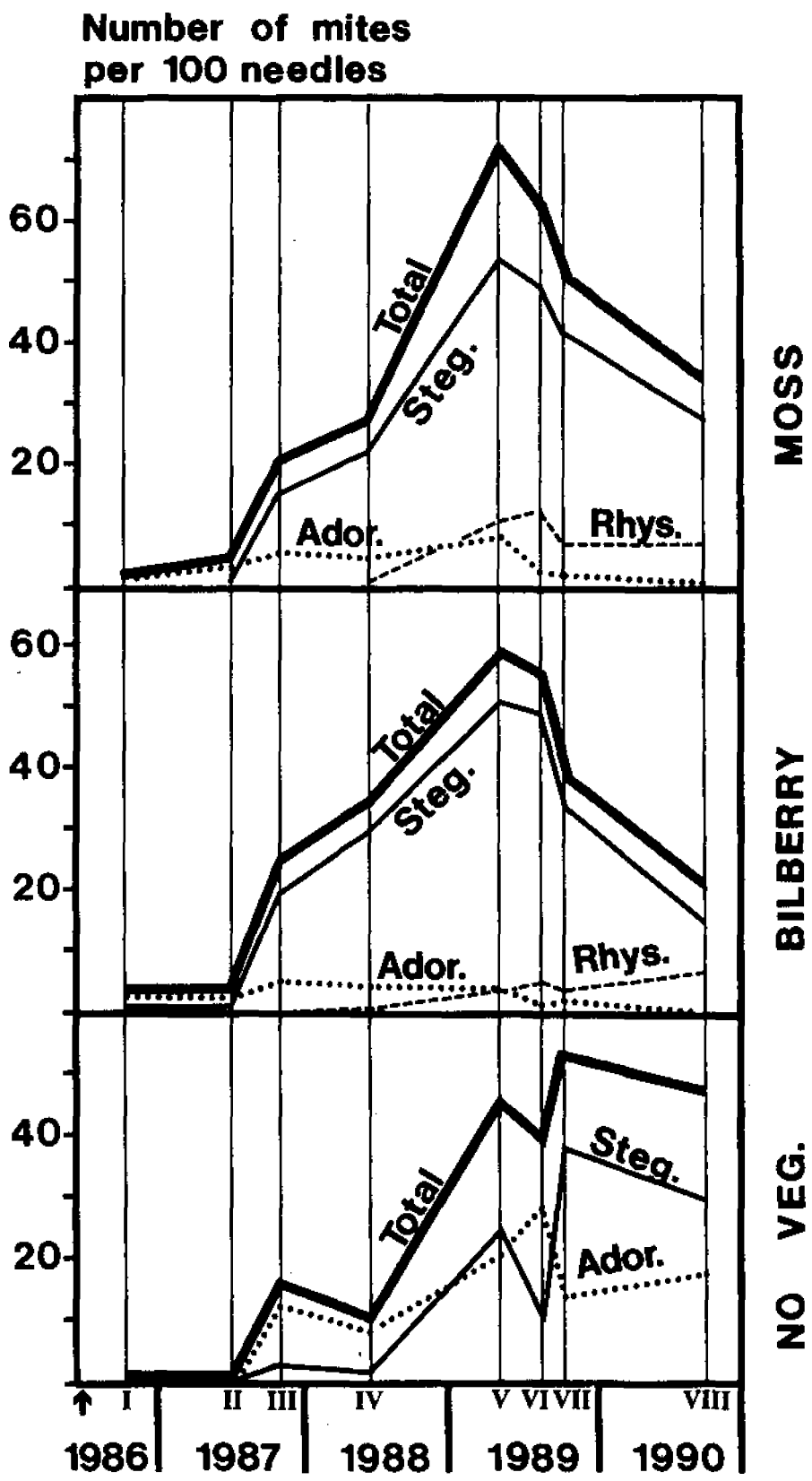

Fig. 9. Numbers of mites per 100 dissected needles in the various vegetation types during the experimental period. Unbroken line: *Steganacarus* cf. *striculus*, broken line: *Rhysotritia ardua*, and dotted line: *Adoristes ovatus*

In the moss and moss/bilberry sites, species occurred together in the needles in a random way. There was no indication that a species avoided a needle which was occupied by another species (based on 800 needles, of which 308 contained mites). However, in the vegetation-free site, the occurrence of *S.* cf. *striculus* and *A. ovatus* together in the same needle was significantly more rare than on a random base (P = 0.0027 for each, based on 600 needles of which 171 contained mites). This means that they either avoid each other, prefer different needles, or prefer different microsites in the forest floor. Fig. 8 gives support to the last explanation, since single strips could contain a high dominance of one species.

Phenology, succession and developmental time

The number of mites per 100 needles throughout the study period (Fig. 9) illustrates some main patterns in phenology and succession. In the moss and bilberry habitats, *S.* cf. *striculus* dominated the picture, with much smaller maximum populations of *A. ovatus* and *R. ardua*. The succession started with a few *A. ovatus* juveniles. Then *S.* cf. *striculus* rapidly took over the dominance. *R. ardua* was a late colonisor, with the first juveniles after three years. In the "no vegetation" site, *R. ardua* was lacking, and the two other species achieved rather similar maximum numbers. Again, *A. ovatus* started the succession by being dominant during the two first years.

In Fig. 10, the phenology of the different developmental instars of each species has been given. The data from the moss and bilberry habitats have been fused because they were very

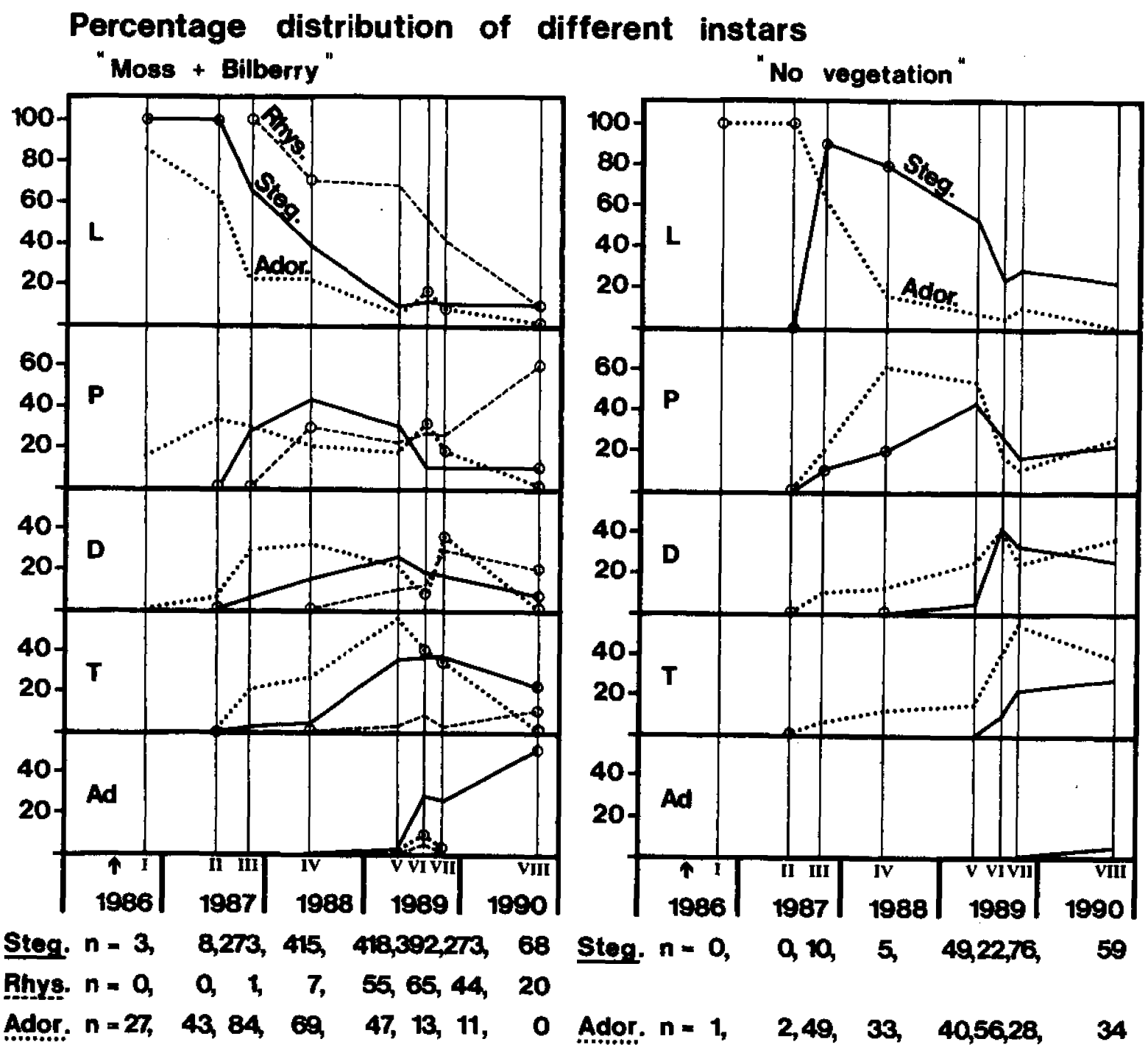

Fig. 10. Phenology of *Steganacarus* cf. *striculus* (unbroken line), *Rhysotritia ardua* (broken line) and *Adoristes ovatus* (dotted line) in moss and bilberry vegetation (fused), and in "no vegetation". The percentage of each developmental stage has been given throughout the study period. L = larva, P = protonymph, D = deuteronymph, T = tritonymph, Ad = adult. Total numbers of individuals at each sampling are given below. Uncertain points due to low n are indicated by small rings at the curves. Data from sampling VIII in moss and bilberry are uncertain due to a biased selection of unfragmented needles, and represent a minimum total frequency of mites

similar. Although the material was limited on certain samplings, a rather consistent picture appears. In moss and bilberry, the succession of the three species was reflected within each developmental stage: *A. ovatus* had a maximum first, then *S.* cf. *striculus,* and finally *R. ardua*. Also in "no vegetation", the pioneer character of *A. ovatus* was evident in the various developmental stages. Within each of the three species, we can follow how the various developmental stages successively appeared and reached their maximum dominance. It is also evident that the phenology of *S.* cf. *striculus* and *A. ovatus* was delayed in the "no vegetation" habitat compared to the moss and bilberry sites.

The large patterns which appear in Fig. 10 are clear enough to describe succession patterns and the gradual occurrence and dominance of the different developmental stages. However, each developmental stage could be found over several years, and all developmental stages were often present at the same time. Obviously, the data do not result from one egg-laying (one cohort) in each species. The occurrence of larvae through several years indicates that egg-laying was spread over years.

While Fig. 10 is based on the relative distribution of the various instars at each sampling, Fig. 11 gives the real numbers per 100 needles. In the moss and bilberry sites, both *A. ovatus* and *S.* cf. *striculus* had rather stable populations of larvae over 2–3 years, indicating a more or less continuous egg-laying over a long period for both species. In fact, larvae of *S.* cf. *striculus* were found at all eight samplings. Even in *A. ovatus*, larvae were recorded in all but the

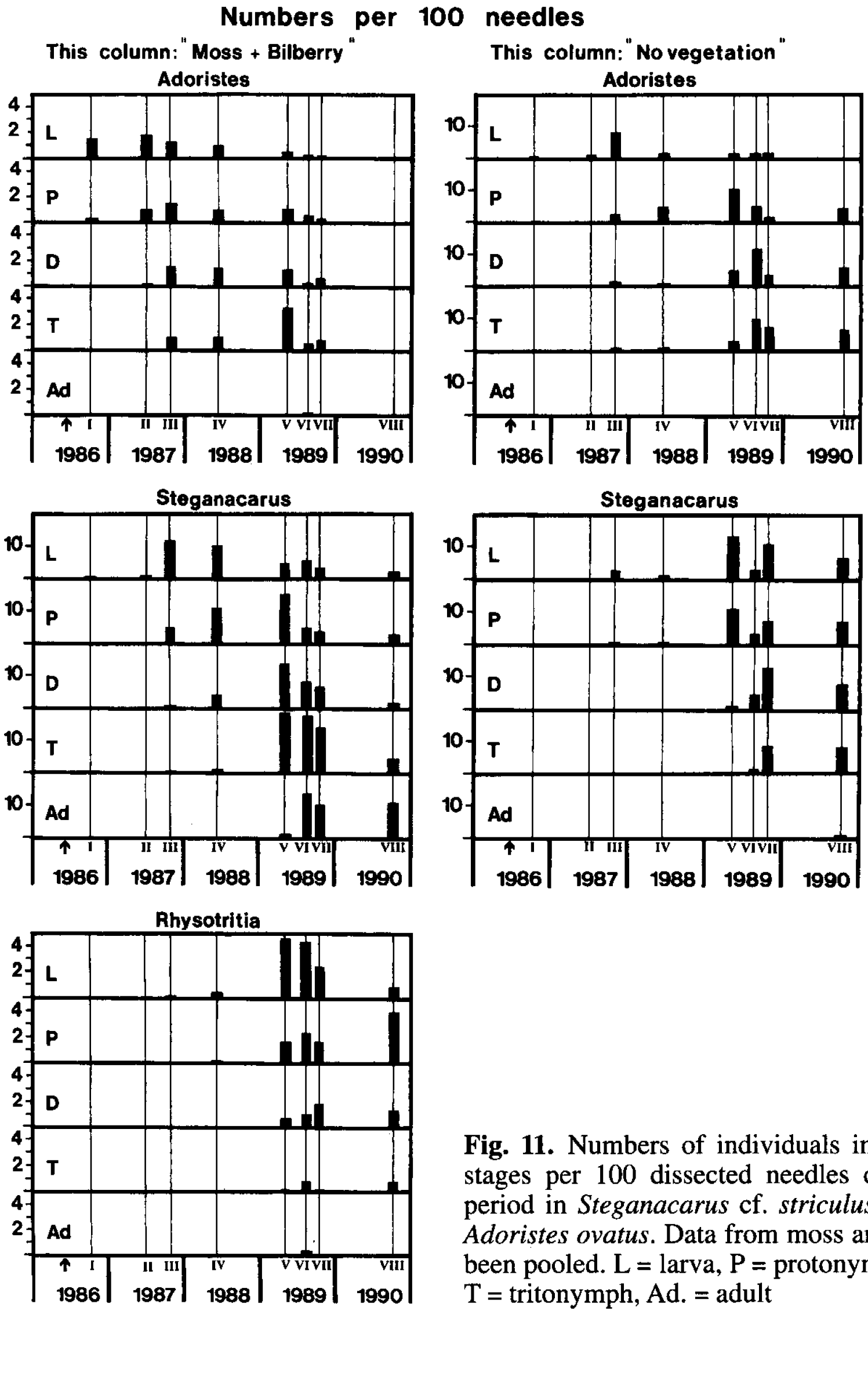

Fig. 11. Numbers of individuals in various developmental stages per 100 dissected needles during the experimental period in *Steganacarus* cf. *striculus, Rhysotritia ardua* and *Adoristes ovatus*. Data from moss and bilberry habitats have been pooled. L = larva, P = protonymph, D = deuteronymph, T = tritonymph, Ad. = adult

last sampling. *R. ardua* sems to have a more concentrated egg-laying after approximately three years. In the "no vegetation" site, larvae of *A. ovatus* showed a maximum abundance at sampling III. The dominance of this cohort is reflected in a maximum abundance of protonymphs in sampling V and deuteronymphs in sampling VI. A more concentrated egg-laying is also indicated for *S.* cf. *striculus* in this habitat. By comparing "moss and bilberry" and "no vegetation", it is clear that the development of both species was considerably delayed in the latter, drier habitat.

Some newly developed adults were recorded inside needles, mainly in the "moss and bilberry" site in 1989, and mainly consisting of *S.* cf. *striculus.* For *A. ovatus* and *S.* cf. *striculus,* this indicates a developmental time of approximately two years, maybe more. No adults were found until the needles had been approximately three years on the ground. The highest

Table 3. Distribution of developmental stages in *Steganacarus* cf. *striculus* after 3–9 months in cultures at 15 °C. Numbers are given for larvae (L), protonymphs (P), deuteronymphs (D) and tritonymphs (T)

Developmental stage	L	P	D	T
3 months	1	8	5	1
5 months	4	1	2	9
7 months				7
9 months				6

numbers of *S.* cf. *striculus* adults were recorded in samplings VI, VII and VIII, which were from late summer (late August to late October). As some were even recorded in May (sampling V), newly developed adults probably appear during the whole season.

Stating that larvae of *S.* cf. *striculus* still may be found four years after the needle were placed in the field, and adding another two years for development, we can conclude that the needles may serve as developmental sites for mites during six years. However, this may be restricted to the most durable needles, which do not fragment during the first years.

The results from the culture at 15 °C are given in Table 3. Although the material was small, the following conclusions can be drawn:

1. The total developmental time must be longer than nine months, since all the recorded animals were tritonymphs at this time.
2. The tritonymph stage seems to last for a long time. Although more than half of the juveniles were tritonymphs after five months, no adults were found four months later.
3. There were great individual variations in the developmental rate. Both after three and five months, all the four developmental stages were present simultaneously.

The limited material from the culture at simulated field temperatures indicated a two year developmental time. After five months (at the start of the first winter), one larva, fourteen protonymphs and one deuteronymph were recorded. This confirms that the developmental rate may vary between individuals. Two mites picked out after 15 months were both tritonymphs, and no free-living adults were observed. After 22 months, a newly developed adult and three tritonymphs were recorded inside needles. Since the temperature during the second winter was slightly higher than natural, and tritonymphs were still present, I would suggest that minimum two years are needed for development.

The effect on decomposition rate

The mean dry weight loss of the needles was much slower in the dry "no vegetation" site than in the moss and bilberry sites (Fig. 12).While the mean dry weight per needle was reduced from about 3.4 mg to about 2.0 mg during three years in the vegetation-free site, the dry weight ended up around 1.0–1.2 mg in the vegetated sites. From samplings III or IV and onwards, needles with or without mites were weighed separately. In the vegetated sites (Moss I and II, Bilberry I and II), needles containing mites were often significantly heavier than needles without mites (Fig. 12). Needles with or without mites in a given strip were usually well separated in dry weight, while different strips might have reached different levels of dry weight loss due to their local position in the forest floor. The apparent increase in dry weight at sampling V in some sites was due to such local differences in decomposition rates.

In the vegetation-free site, however, no consistent picture appeared, although needles with animals were significantly heavier in one instance (sample VII, Fig. 12).

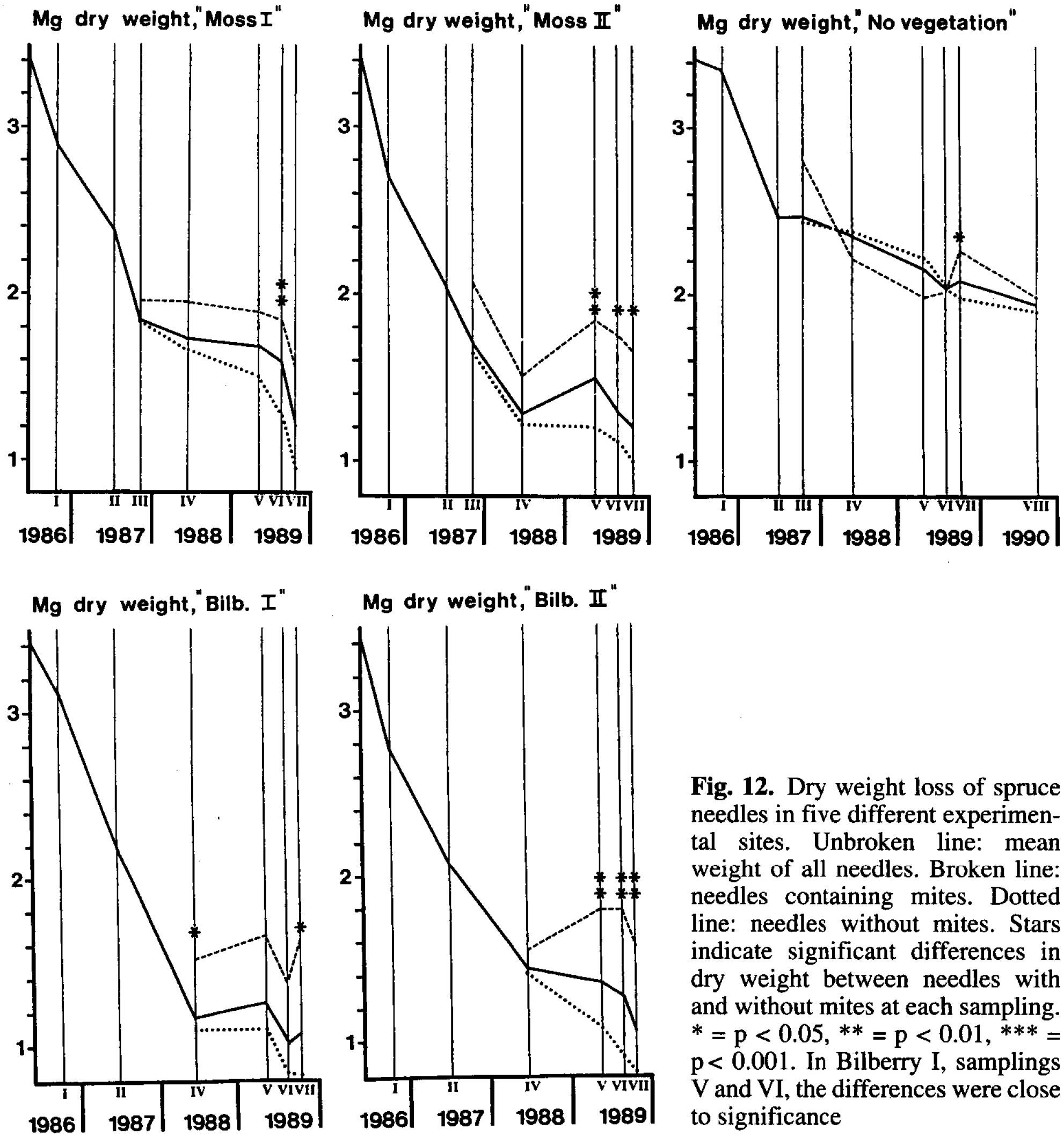

Fig. 12. Dry weight loss of spruce needles in five different experimental sites. Unbroken line: mean weight of all needles. Broken line: needles containing mites. Dotted line: needles without mites. Stars indicate significant differences in dry weight between needles with and without mites at each sampling. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$. In Bilberry I, samplings V and VI, the differences were close to significance

Discussion

Biology of the species

The biology of *A. ovatus* has been thoroughly studied in France, where it developes within decomposing needles of *Abies alba* Mill. (Gourbiere et al. 1985, Lions & Gourbiere 1988, 1989). About 50 % of the needles were colonised, with spatial variations between 30 and 70 %. There was only one cohort of *A. ovatus* eggs laid in needles which had been approximately one year on the ground. As observed in the present study, some eggs were placed in the cracks created by *Lophodermium piceae* but most were laid at the petiole (the attachment end of the needle) so that the juvenile started to excavate from that end of the needle. Individual developmental rates varied, however, so that some adults appeared after one year, and some after two years.

Under Norwegian conditions, with a colder climate and a slower decomposition rate, the development of *A. ovatus* seems to take at least two years, and egg-laying occurs in needles of very different age (larvae were present during three years, Fig. 11). The combination of a long and probably very individual developmental time, and an extended egg-laying period created a mix of developmental stages so that all juvenile stages of *A. ovatus* were found simultaneously during three years (1987–1989, Fig 11.). The situation was quite parallel in *S.* cf. *striculus* (Fig. 11). The culture of the last species at 15 °C confirmed both a very slow and highly variable developmental rate, and no adults had developed after 9 months (Table 3). The culture at simulated field temperatures indicated that the species needs two years or more for full development.

Although all juvenile stages of these two species were present simultaneously during three years, Fig. 10 shows that different developmental stages succesively dominated as the years went on. This pattern probably reflects a maximum in egg-laying intensity after 1–2 years in the vegetated sites for *A. ovatus* and *S.* cf. *striculus*.

Only a few *A. ovatus* adults were recorded inside needles, in contrast to numerous adults os *S.* cf. *striculus*. According to Lions & Gourbiere (1988), adults of *A. ovatus* leave the needle shortly after the last moulting. The light colour of most adult *S.* cf. *striculus* found within needles indicates that this species needs a longer time for the exoskeleton to harden.

The life within the needle is very safe from predators, and these mites may probably be classified as K-strategists. Even though this study is based on frozen material, the impression was that mortality among juveniles was very low. When excrements were found, an intact animal was almost always present. Gourbiere et al. (1985), who dissected out living animals of *A. ovatus* from *Abies alba* needles, estimated a total mortality of 20 %. Even this value is relatively low. A disadvantage of this life form is a slow developmental rate, which may be due to a low food quality. While free-living microarthropods can graze selectively on the microflora, the gut contents of juveniles among the three studied species contained fine-grained brown material of the inner needle tissue. There was no indication that the juveniles selectively grazed on fungal hyphae growing within their cavity. Their feeding apparatus, with claw-formed chelicera, is evidently designed for digging and excavating.

Although the needles were placed from the beginning in rather moist conditions in the moss layer, very few mites colonised during the first year. As cracks made by *Lophodermium piceae* were numerous on the needle surfaces in this habitat already after four months, possibilities of egg-laying were theoretically present very early. The needles might also have to be "conditioned" by the microflora before the juveniles can digest the content. However, it is an open question whether they digest the substrate directly, the microflora in it, or both. The "timing" of egg-laying is important, because after a certain time, most of the inner substrate of the needle may be consumed by the microflora. For some reason, *R. ardua* chooses older needles than the two other species. Also Kaneko (1990) and Fukuyama & Ito (1992) found that *R. ardua* uses relatively old needle litter in Japan.

Other studies support the assumed long duration of the tritonymph stage of *S.* cf. *striculus* (cf. Table 3). For both *Steganacarus magnus* (Nicolet) and *Phthiracarus piger* (Scopoli), the tritonymph is the stage with the longest duration. Great individual variations in developmental time has also been noted in *S. magnus* (Webb 1977, Berg 1989).

Ecological flexibility within species, but still ecological segregation between species

A key word for mites with this life form is flexibility. With their limited individual mobility, but still with a considerable geographical distribution, each species should be able to use different substrates of litter, and adjust reproduction rythms and developmental rates to local climatic and food conditions. The flexibility for substrates is evident already at the micro-level, as colonised spruce needles may vary considerably in their degree of decomposition, inner

structure and fungal flora. These factors may also vary within different sections of the same needle. Such variations, and also the presence of more than one individual in the same needle, may explain the great individual variations in developmental rate. Since the juveniles do not seem to change needles during their development, each animal is "trapped" within its needle and depends wholly on the local food conditions.

Several cryptic-living mites can use litter of very different kinds. For instance, *R. ardua* can use bark pieces of both yellow birch and hemlock, and even heart wood of twigs of yellow birch (Wallwork 1957). *Steganacarus magnus* can develop both within pine cone scales (Webb 1977) and in beech cupules (Harding & Easton 1984). This means that conclusions about substrate, phenology and abundance cannot be uncritically transferred from one country to another.

On the other hand, in a given ecosystem, species with similar life forms have to be ecologically separated in some way. In the present study site, three species share the niche of developing inside spruce needles. However, already at the "macro-level", the following differences between species can be seen: *R. ardua* was absent from the dry, vegetation-free sites, while *A. ovatus* preferred that environment. *S.* cf. *striculus* occurred numerously both places, with a preference for the moss-covered environment (Fig. 9). *A. ovatus* was the earliest colonizer of the three, while *R. ardua* came late in the succession (Figs. 10–11). At the "micro-level", it was shown that two, and even three, species could occur within the same needle. There was no statistical indication from the moss-covered site that one species could detect that the needle was already occupied by another. The presence of very different developmental stages of the same species within one needle furthermore indicates that an egg-laying female may not distinguish between occupied and non-occupied needles within its own species. Since less than half of the needles were colonised by mites, and three individuals may develop within one needle, this random egg-laying may not create serious competition between species. However, in the vegetation-free areas, different strips often had a clear dominance of either *A. ovatus* or *S.* cf. *striculus* (Fig. 8). This indicates a certain horizontal segregation of the species, perhaps with the former species in the driest local patches.

Effects on decomposition rate

After three years, about 39 % of the needles had been colonised by mites in the moss and bilberry sites (Table 1, mean value of samplings V–VII). In these vegetated sites, dry weight loss was, on average, 28 % slower in needles with mites than in needles without mites (sampling VII, Moss I: 25 %, Moss II: 27 %, Bilberry I: 31 %, and Bilberry II: 29 %). In the actual study site, needles represent 55 % of the dry weight of the litter fall from trees (Røsberg 1991, mean value of three years). If other types of tree litter (mainly cones and twigs) decompose at a rate similar to that of needles, the total retarding effect of the mites on the decomposition rate of tree litter would be $28\,\% \times 0.39 \times 0.55 = 6.0\,\%$. This means that the presence of these mites may significantly retard the total decomposition rate of tree litter during the three first years. Since a considerable part of the total litter during the actual period consisted of cones, which decompose very slowly (Hågvar, unpubl.), 6 % is probably an underestimation. Data from 14 spruce forest sites in south Norway show that needles represent from 55 to 86 % of the tree litter dry weight on a yearly basis, much depending on the local amount of cone litter. On average, 74 % of the dry weight of the litter was needles (Mork 1942, Bonnevie-Svendsen & Gjems 1957, Røsberg 1991). If the present data about mite colonisation in needles are representative, the retarding effect of the mites in a typical spruce forest would be minimum $28\,\% \times 0.39 \times 0.74 = 8.1\,\%$. The total effect on the ecosystem would, however, be lower because of the additional litter input from ground vegetation and dead roots.

Since there were no consistent effects of the mites in the vegetation-free site where *A. ovatus* was abundant, the retarding effect may be linked to the activity of *S.* cf. *striculus,* which dominated completely in the vegetated sites.

Berg et al. (1980) found that the presence of adult "box mites" (*Phthiracarus* spp. and *R. ardua*) could reduce the decomposition rate of pine needles. They suggested that the adult mites in some way interacted with the microflora. In the present case, where juveniles develop inside needles, an explanation of the retarding effect may be that excrements of box mites are resistant to decomposition. This is apparently the case, as small and large excrements of different age within a needle seem to be rather intact. Pande & Berthet (1973) made detailed studies of the soil microstructure in a black pine plantation by studying 2 mm thick soil sections. They concluded that faecal pellets of Oribatei decomposed very slowly, and that pellet congregations were usually not colonized by fungi. Obviously, the decomposition rate of *Steganacarus* excrements should be further studied, both when they are locked within the needle, and after the fragmentation of the needle.

One is tempted to ask whether the juvenile mite produces antimicrobial agents in order to avoid competition with the microflora for the limited resources within the needle, and that this may reduce the decomposition rate of both the needle matrix and the excrements.

While the mites significantly retard the decomposition rate of spruce needles during the early decomposition phases, this may perhaps be counteracted during later phases. In a litter bag study where decomposing spruce needles were followed for ten years (Hågvar 1991), the population of adult *Steganacarus* sp. was high after five years. At this time, many needles had been excavated by juveniles, and the needles in general started to fragment. The opening of the more or less excavated needles with cavities and excrements may create a number of new habitats and niches, both for soil animals and the microflora, and a dense network of hyphae was observed at this time. While the smaller microarthropods had largely refused to colonise the needle litter up to this stage, these species colonized numerously after the needles had fragmented. In fact, the total abundance of Collembola and Oribatei was higher after ten years than after five years. It could be that needles inhabited by box mites decompose more rapidly than other needles when they reach the fragmented phase where the microhabitats within them are made available to other organisms.

A number of studies have indicated that microarthropods generally increase the decomposition rate (review by Seastedt 1984). A microcosm study with the present type of needle-dominated raw humus showed that the presence of microarthropods (including *S.* cf. *striculus*) and enchytraeidae usually increased the decomposition rate compared to samples containing only microflora (Hågvar 1988). Although excavating mites obviously can retard decomposition during the first years, it is an open question whether the total decomposition process is delayed by their presence.

A laboratory study during two weeks at 20 °C showed that free-living adults of *S.* cf. *striculus* may bore into and excavate spruce needles. The needles in this case had been collected on snow, kept dry and remoistened. Clearly, adults also contribute to needle fragmentation and excrement production. Since this type of feeding marks were not regularly observed during the present study, it may be that adults normally feed in the lower layers where they emerge, and then migrate up to fresher needles in the litter layer to deposit the eggs.

Maybe the activity of these mites can have some advantages in the system, for instance, if their resistant excrements increase the water-holding capacity of the raw humus. Zachariae (1963) and Pande & Berthet (1973) indicated that microarthropod excrements may contribute significantly to humus production, to reduce the leaching process and thus ensure a slow but steady supply of nutrients to plants.

Most decomposition studies have concentrated on the early phases, and the known effects of animals and microflora are often limited to these. Several substrates, however, including coniferous needles, decompose very slowly. In the litter bag study of Hågvar (1991), spruce needles still had about 25 % dry weight left after ten years, and the process probably goes on for decades. A complete understanding of decomposition rates and the role of various soil organisms demands that more effort is spent in studying the late decomposition phases. Here lies also the key to humus formation, which is so important for both water and nutrient budgets.

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References

Abrahamsen, G. (1972a) Ecological study of Lumbricidae (Oligochaeta) in Norwegian coniferous forest soils. Pedobiologia **12**, 267–281.

Abrahamsen, G. (1972b) Ecological study of Enchytraeidae (Oligochaeta) in Norwegian coniferous forest soils. Pedobiologia **12**, 26–82.

Berg, B., Lohm, U., Lundkvist, H., Wirén, A. (1980) Influence of soil animals on decomposition of scots pine needle litter. In: Persson, T. (ed) Structure and Function of Northern Coniferous Forests. An Ecosystem Study. Ecological Bulletins (Stockholm) **32**, 401–409.

Berg, J. (1989) Zur Biologie und Taxonomie der Phthiracaroidea (Acari: Oribatei) in einen Buchenwald. Thesis, Karlsruhe University, 151 pp.

Berg, J. (1991) Distribution pattern and phenology of Phthiracaridae and Euphthiracaridae (Acari: Oribatei) in a beech forest. In: Dusbábek, F., Bukva, V. (eds) Modern Acarology. Academia, Prague and SPB Academic Publishing bv, The Hague, Vol. **2**, pp. 521–527.

Bonnevie-Svendsen, C., Gjems, O. (1957) Amount and chemical composition of the litter from larch, beech, Norway spruce and Scots pine stands and its effect on the soil. Reports of The Norwegian Forest Research Institute **XIV**, 111–174.

Fukuyama, K., Ito, M. (1992) Succession of Oribatid mites (Acari: Cryptostigmata) community in soil and in needle litter after reforestation of *Cryptomeria japonica* in Japan. Journal of The Acarological Society of Japan **1(2)**, 113–126.

Gourbière, F., Lions, J. C., Repin, R. (1985) Activité et développement d'*Adoristes ovatus* (C. L. Koch, 1839) (Acarien, Oribate) dans les aiguilles d'*Abies alba* Mill. Relations avec la décomposition et les microflores fongiques. Revue d'Écologie et de Biologie du Sol **22**, 57–73.

Hågvar, S. (1982) Collembola in Norwegian coniferous forest soils I. Relations to plant communities and soil fertility. Pedobiologia **24**, 255–296.

Hågvar, S. (1988) Decomposition studies in an easily-constructed microcosm: Effects of microarthropods and varying soil pH. Pedobiologia **31**, 293–303.

Hågvar, S. (1991) Succession of microarthropods in decomposing spruce needles: A litter bag study over ten years. In: Veeresh, G. K., Rajagopal, D., Viraktamath, C. A. (eds) Advances in management and conservation of soil fauna. Oxford & IBH Publishing Co. PVT. LTD., New Delhi, Bombay, Calcutta, pp. 485–489.

Hågvar, S., Amundsen, T. (1981) Effects of liming and artificial acid rain on the mite (Acari) fauna in coniferous forest. Oikos **37**, 7–20.

Harding, D. J. L., Easton, S. M. (1984) Development of two species of Phthiracarid mites in beech cupules. Acarology **VI**, Vol. **2**, 860–870.

Hartenstein, R. (1962) Soil Oribatei VII. Decomposition of conifer needles and deciduous leaf petioles by *Steganacarus diaphanum* (Acarina: Phthiracaridae). Annals of The Entomological Society of America **55**, 713–716.

Jacot, A. P. (1939) Reduction of spruce and fir litter by minute animals. Journal of Forestry **37**, 858–860.

Johansson, M.-B. (1994) The influence of soil scarification on the turn-over rate of slash needles and nutrient release. Scandinavian Journal of Forest Research **9**, 170–179.

Kaneko, N. (1990) Decomposition process of needle litter of Japanese Red Cedar (*Cryptomeria japonica*) by oribatid mites. Journal of The Japanese Forestry Society **72(2)**, 158–162. (In Japanese)

Lions, J. C., Gourbière, F. (1988) Populations adultes et immatures d'*Adoristes ovatus* (Acarien, Oribate) dans les aiguilles de la litière d'*Abies alba*. Revue d'Écologie et de Biologie du Sol **25**, 343–352.

Lions, J. C., Gourbière, F. (1989) Populations d'*Adoristes ovatus* (Acarien, Oribate) vivant à l'extérieur des aiguilles dans la litière d'*Abies alba*. Revue d'Écologie et de Biologie du Sol **26**, 213–223.

Mork, E. (1942) Über den Streufall in unseren Wäldern. Eine Analyse der Menge und des chemischen Gehalts von Waldstreu und der dieselben beeinflussenden Faktoren. Reports of The Norwegian Forest Research Institute **VIII**, 297–365. (In Norwegian with German summary)

Pande, Y. D., Berthet, P. (1973) Studies on the food and feeding habits of soil Oribatei in a black pine plantation. Oecologia **12**, 413–426.

Ponge, J.-F. (1988) Etude écologique d'un humus forestier par l'observation d'un petit volume. III. La couche F_1 d'un moder sous *Pinus sylvestris*. Pedobiologia **31**, 1–64.

Røsberg, I. (1991) Deposisjon av næringsstoff med strø og nedbør i granbestand på Nannestad, Akershus. In: Bretten, S., Krovoll, A. (eds) Symposium in vegetation ecology at Kongsvold 1990 and 1991. Universitetet i Trondheim, Vitenskapsmuseet, Rapport Botanisk Serie **1991 (2)**, 136–155. (In Norwegian)

Seastedt, T. R. (1984) The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology **29**, 25–46.

Wallwork, J. A. (1967) Acari. In: Burges, A., Raw, F. (eds) Soil biology. Academic Press, pp. 363–396.

Webb, N. R. (1977) Observations on *Steganacarus magnus*. General biology and life cycle. Acarologia **XIX**, 686–696.

Zachariae, G. (1963) Was leisten Collembolen für den Waldhumus? In: Doeksen, J., Drift, J. van der (eds) Soil organisms. Amsterdam, North-Holland, pp. 109–124.